Liu, A. G. S. C., McIlroy, D., Matthews, J., & Brasier, M. D. (2014). Confirming the metazoan character of a 565Ma trace-fossil assemblage from Mistaken Point, Newfoundland. PALAIOS, 29(8), 420-430. 10.2110/palo.2014.011

CONFIRMING THE METAZOAN CHARACTER OF A 565 MA TRACE FOSSIL ASSEMBLAGE FROM MISTAKEN POINT, NEWFOUNDLAND

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RRH: EDIACARAN TRACE FOSSILS

LRH: LIU ET AL.

Keywords: Ediacaran, Avalonia, ichnology, evolution, Newfoundland

ABSTRACT

Surface locomotory trace fossils from the Mistaken Point Formation of Newfoundland, dated at ~565Ma, suggest that organisms capable of controlled locomotion and possessing muscular tissue may have existed amongst Avalonian Ediacaran macrofossil assemblages. Here we describe the Mistaken Point trace fossil assemblage in full, discuss its stratigraphic context within the Mistaken Point Formation, and explore the competing hypotheses for the formation of the traces. We find that the trace fossils, preserved within a turbidite succession in a deep-marine depositional environment, are

not attributable to abiogenic structures, to Ediacaran tubular or filamentous body fossils, to rangeomorph stems, or to a host of late Ediacaran and early Phanerozoic ichnofossils. Specimens within the assemblage show some similarities to the ichnogenera *Helminthoidichnites* and *Archaeonassa*, but discrepancies in certain aspects of their structure mean that we do not formally attribute them to these ichnotaxa at this time. The Mistaken Point ichnofossils possess morphological characteristics indicative of formation by an organism with a round base. Comparison with traces formed by modern organisms of such character appears to rule out formation by protistan, echinoderm, or annelid styles of movement, but is consistent with organisms moving via muscular controlled locomotion in a similar way to some modern molluscs and actinian cnidarians. We suggest therefore that the Mistaken Point trace fossil assemblage reveals the presence of muscular metazoans in late Ediacaran deep-marine ecosystems. Such organisms cannot yet be attributed to specific phyla, but their inferred locomotory mechanisms share closest similarities with those utilised by extant actinians.

INTRODUCTION

The Ediacaran strata of eastern Newfoundland and the United Kingdom contain some of the oldest macrofossils in the geological record, dated at between 579 and ~556 Ma (Ford, 1999; Compston et al., 2002; Van Kranendonk et al., 2008; Wilby et al., 2011). These regions are considered to have lain on the margins of the micro-continent of Avalonia during the late Ediacaran Period (Landing, 1996). Avalonian fossil assemblages record a variety of soft-bodied organisms, widely termed the Ediacaran biota, which have proven difficult to classify within modern biological groups (e.g., Laflamme et al., 2013). Body fossils of the Avalonian Ediacaran taxa range from a few millimeters (Liu et al., 2012) to over a meter in size

(Narbonne and Gehling, 2003), and are most commonly preserved as moulds or casts at the interface between volcanic tuffs/volcaniclastic event beds, and underlying pelagic/hemipelagic mudstones and siltstones (e.g., Narbonne, 2005). Avalonian fossil assemblages largely record life in deep-marine depositional paleoenvironments (Wood et al., 2003), and are dominated by members of the Rangeomorpha, a high-order taxonomic group of sessile, benthic, frond-like forms that exhibit considerable morphological diversity (Narbonne, 2004; Brasier et al., 2012; Laflamme et al., 2013), but whose phylogenetic interpretation remains to be resolved.

The discovery of horizontal surface traces up to 13 mm in width and 17 cm in length in the deep-water successions at Mistaken Point, Newfoundland (Liu et al., 2010a) forced reconsideration of earlier interpretations (e.g., Seilacher, 1992) of the Avalonian benthic ecosystems as being composed entirely of sessile taxa. Our initial documentation of these trace fossils established their biogenicity, and briefly explored possible analogues for the physical locomotory methods utilised by the trace makers (Liu et al., 2010a, 2010b). The late Ediacaran ichnofossil record has since been supplemented by additional reports of locomotory activity (e.g., Chen et al., 2013; Menon et al., 2013). However, significant debate surrounds the validity of an ichnological interpretation for recently proposed bioturbation at ~555 Ma documented by Rogov et al. (2012), which is contested by Brasier et al. (2013b). Possible evidence for metazoan locomotion at ~585 Ma (Pecoits et al., 2012) has similarly been cast into doubt (see Gaucher et al., 2013). Amid such discussions, we here describe the ichnology and sedimentology of the trace-fossil bearing surface at Mistaken Point in greater detail. We document in full the morphological variability within the ichnofossil assemblage, and provide further evidence to support the ichnological interpretation of this important material.

THE MISTAKEN POINT TRAIL BED

The trace-fossil bearing horizon is located within the Mistaken Point Ecological Reserve, on the south-eastern coast of Newfoundland, Canada (Fig. 1). The surface lies within the uppermost Mistaken Point Formation, on the southern side of Mistaken Point, a world-renowned site for Ediacaran macrofossils that was first brought to global attention in the late 1960s (Anderson and Misra, 1968; Misra, 1969). The trace-fossil bearing horizon has not yet been dated by radiometric techniques, since the tuff immediately above it is thin (1 mm), difficult to access, and deeply weathered. The closest age constraint comes from a tuff some 53 m stratigraphically below the trace-bearing bed, which smothered a diverse macrofossil assemblage (e.g., Clapham et al., 2003). This tuff has been dated by U-Pb geochronology to 565±3 Ma, although the data has thus far only been published in abstract form (Benus, 1988)

The Mistaken Point trace fossils are found on a narrow ledge within a thick succession of siliciclastic sediment gravity flows. The depositional environment is interpreted to have been a deep-marine slope within a fore-arc basin, adjacent to active volcanic centers (see Wood et al., 2003; Ichaso et al., 2007; Liu et al., 2010b). The preservation of partial Bouma successions alone is not conclusive evidence of deep-marine paleoenvironments; turbidite-like hypopycnal flows are well known in prodelta, shoreface, and lacustrine successions (e.g., Dyni and Hawkins, 1981; Nelson, 1982; Pattison, 2005). However, the presence of a ~2000 m thick succession of turbiditic strata without evidence for demonstrably shallow-water or lacustrine sedimentary structures argues against a shallow-marine depositional environment (cf. Narbonne et al., 2005). Sphaeromorphic acritarchs and filamentous microfossils have been documented in units stratigraphically above and below the Mistaken Point Formation across southeastern Newfoundland (Hofmann et al., 1979), including from units containing diverse Ediacaran macro-organisms (e.g., the Fermeuse Formation of the Bonavista Peninsula; Hofmann et al., 2008). Such simple carbonaceous

remains cannot however be used for paleoenvironmental analysis. At present, all available sedimentological and paleontological evidence is consistent with deposition in a marine setting with episodic deposition of sediment from turbidite-like waning flow currents (Liu et al., 2010b).

The trace-bearing surface sits above an 18 cm-thick, normally-graded bed consisting of a sandstone-to-mudstone T_{acde} turbidite (cf. Bouma, 1962; Fig. 2). Paleocurrent directions determined from ripple cross-lamination within the T_c component of this bed are broadly consistent with those obtained from other Mistaken Point Formation beds in this region, implying current flow typically towards the southeast (Wood et al., 2003). Unit T_e is comprised of both turbiditic hemipelagite and pelagite, with the uppermost 3 mm being an unlaminated, green-weathering mudstone (cf. Brasier et al., 2013a). The trace fossils lie on the upper surface of this mudstone (Fig. 2). The bedding plane is overlain by a coarse-grained 1mm-thick brown tuff that contains euhedral, but often oxidised and weathered, pyrite crystals, and this is itself overlain by a fine-grained sandstone turbidite. This pyrite, presumably a result of early diagenetic processes, provides evidence against prolonged sub-aerial exposure of this surface (contra Retallack, 2010). The total exposed area of the ichnofossil-bearing surface is approximately two square meters, significantly smaller than that of the neighboring famous fossil-bearing bedding planes (e.g. the ~131 m^2 Mistaken Point 'E' Yale Surface).

Preservation of trace fossils cast beneath the volcanic tuff is consistent with the "Conception-type" cast-and mould style preservation of body fossils seen in adjacent beds (cf. Narbonne, 2005). This implies that the general taphonomic conditions acting upon this bed were not dissimilar to those that commonly preserved soft-bodied Ediacaran organisms elsewhere within the Mistaken Point Formation.

DESCRIPTION OF THE TRACE FOSSIL ASSEMBLAGE

The trace fossil-bearing horizon has been fully mapped in order to document all possible biological impressions (Supp. Figs S1.1–S1.15). Casts of the most interesting regions of the surface are housed in the Oxford University Museum of Natural History under accession numbers OUM ÁT.418/p to OUM ÁT.423/p. The assemblage consists of eighty two possible linear trace fossils, with dimensions ranging between 6–198 mm in length, and 1–14 mm in width. The potential trace fossils most commonly consist of a negative epirelief groove running along the surface of the sediment, bounded by positive epirelief marginal ridges (Fig. 3). These ridges provide key evidence for sediment displacement that we infer to have resulted from movement along the sediment surface (cf. Jensen et al., 2005, 2006). The surficial nature of the structures can be used to distinguish trace fossils from superficially similar abiogenic structures such as cleavage, desiccation cracks, and intrastratal shrinkage (formerly synaeresis) cracks (Parizot et al., 2005; Harazim et al., 2013). The trace fossils neither branch nor bifurcate, and do not exhibit any systematic changes in width such as characterizes many tubular body fossils (Liu et al., 2010a) and drag marks.

1. Specimens with transverse ridges

Twenty nine of the potential trace fossils show evidence of internal structure in the form of raised transverse ridges of siltstone (e.g. Fig. 3B, D). These specimens range from 1–11 mm in width, and 25–166 mm in length. The transverse ridges that cross the medial groove are mostly crescentic, and occur in series along the full length of the trace at intervals of ~1 mm. Transverse ridges can exhibit variable spacing, and also minor variability in width (e.g. Fig.

3D). An important feature of several of the trace fossils is the presence of a negative epirelief pit, of equal diameter to the corresponding trace, at one end of the linear impression (Fig. 3B–D). Where the associated linear trace fossil has crescentic transverse ridges, the concave edges consistently face the terminal disc. This observation, combined with the close spatial relationship with these crescents, implies that the disc is related to the linear impressions, and probably represents the basal impression of a trace maker (i.e. a resting trace). The crescentic structures are inferred to have been left by the posterior edge of the trace maker as it moved over the sediment (with anterior impressions being removed by each subsequent movement). The traces can be either straight or gently curved (Fig. 3). Although the assemblage as a whole exhibits a preferred trace orientation on the surface (Fig. 4B), when only those specimens with transverse ridge structures are considered, the axial orientations of the traces on the surface are distributed in all directions (Fig. 4A), and are not associated with the orientation of tectonic compression (as evidenced by the short axes of the discs plotted in Fig. 4C). The traces are unevenly distributed along the entire length of the exposed ledge. Where they interact, it is clear that they truncate (cut across) one another (Fig. 3C–D), as opposed to being superimposed on top of each other, or showing other avoidance behavior.

2. Specimens lacking transverse ridges

Impressions possessing neither internal ornament nor terminal discs (e.g. Fig. 3A, S2.6) are also reported from the surface (n = 53). Such impressions typically consist of individual negative-relief troughs running along the surface of the bedding plane, up to 198 mm in length and 1–7 mm in width (though mostly ≤ 4 mm wide). Marginal positive epirelief ridges of sediment are present in around half of such specimens (n = 25), but there is no evidence for transverse ridges of sediment within the longitudinal groove. A handful of impressions are preserved entirely in positive epirelief (e.g. Supp. Fig. S2.4), which may imply that they were

not formed directly on the surface but slightly beneath, or within a microbial mat (cf. Seilacher, 1999). This suggestion may be supported by the presence of a solitary *Aspidella* fossil (likely to be a rangeomorph holdfast) on this surface (Fig. S2.5), with no evidence for preservation of the rest of the organism, which presumably lay at a higher sedimentary level. There is, however, no clear evidence at present for microbial mat fabrics, textured organic surfaces, or microbially induced sedimentary structures on this bedding plane. It is noted that several of these non-ornamented impressions are aligned with the direction of tectonic strain (Fig. 4B–C), and therefore a small subset of the structures could be of tectonic origin.

3. Complex clustering?

One interesting feature is a collection of nine trail-like structures that lack transverse ridges and are concentrated around four small central depressions (Fig. 5). Some of these linear features (at left in Fig. 5) appear to loop back towards the central region, and are independent of all fractures and mineral veins running along the surface. There is, however, little in the way of obvious structure or pattern to these impressions, and their origin and ichnological affinity remains uncertain. This association is the densest accumulation of ichnofossil-like structures observed on the available bedding surface. Protective legislation at the site prevents collection and sectioning of these impressions to determine whether they possess a vertical expression. The most similar ichnotaxon in terms of age, tolerance of deep-marine environmental conditions, and gross morphology (with individual trails looping back towards a central region), is the lower Cambrian *Oldhamia geniculata* (e.g. Seilacher et al., 2005, figs. 7, 12D, 18), although there are substantial differences between our material and this ichnospecies, not least the absence of any complete loops, the less regular spacing of individual looping impressions, and the observation that our material is an order of magnitude larger than typical *O. geniculata* (Fig. 5).

4. Isolated pits

Alongside the linear traces, eleven ovate to circular pits occur on the surface. These are 6–19 mm in long-axis diameter, and possess no internal structure. Pits are of similar appearance, relief, and dimensions to the discoidal impressions found at the end of some of the trace fossils, but are not directly associated with them (see Liu et al., 2010a, fig. 3A–B). All but one of these pits are elongated in broadly the same direction (ENE–WSW), suggesting that elongation is tectonic in origin (mean elongation = 1.616, $1\sigma = 0.23$; Fig. 4C). Given the similarities between isolated pits and those found associated with the traces, it is considered that the isolated pits represent the preserved lower surfaces (be they resting traces or 'body fossil' impressions of the base) of the organisms responsible for creating the trace impressions.

DISCUSSION

We consider that the linear impressions from Mistaken Point described herein were not formed by sedimentological, erosional or tectonic processes (Liu et al., 2010a, 2010b). Mineral veins of quartz cut vertically through the bed in places, but although they show a variety of surface expressions—even where the vein itself is not visible (Supp. Fig. S2.1)—they do not exhibit the characteristic traits of the candidate traces. Most notably, evidence for sediment displacement in the form of marginal ridges, a variety of orientations on a deep-water bedding plane, and rounded rather than angular extremities, support a trace fossil interpretation over abiogenic alternatives (cf. Jensen et al., 2005).

The claim by Retallack that the assemblage might represent tool marks known only from extremely shallow water depositional environments (Retallack, 2010; cf. Wetzel, 1999,

219 2013) is unlikely for two reasons. First, tilting traces, and the vast majority of tool marks, do
220 not typically show sharp turns or bending, and proceed in a linear fashion (Wetzel, 2013);
221 observations that are incompatible with several of the impressions we describe from this
222 assemblage (e.g. Figs. 3D, 5). Secondly, the depositional environment was unequivocally not
223 sufficiently shallow for the formation of such 'tilting traces'. The depth of deposition for the
224 Mistaken Point Formation has been questioned on the grounds of a perceived absence of
225 pyrite, the presence of carbonate concretions, supposed oscillation ripples of shallow-water
226 sedimentary origin, and various geochemical proxies (Retallack, 2010). However, each of
227 these observations can be disputed and explained within a deep-marine depositional regime
228 subject to later compressional tectonism (Liu et al., 2010b and references therein). To date,
229 there is no convincing evidence of even marginal-marine transitional sediments found
230 anywhere within the Mistaken Point Formation in Newfoundland. Furthermore, even if the
231 environment was suitably shallow to permit the preservation of 'tilting traces' (cf. Wetzel,
232 2013), there remain several morphological arguments against such an explanation, such as the
233 observed variation in orientations of the Mistaken Point structures (Fig. 4; Table 1; cf.
234 Wetzel, 2013).

235 Although adjacent bedding planes with identical lithologies and similar taphonomic
236 histories preserve abundant Ediacaran body fossils, the trace fossils and small pits are the
237 dominant forms found on the trace fossil bearing bed. A detailed search of the exposed
238 bedding plane for body fossils revealed only one larger discoidal impression, which is
239 considered to be a holdfast of an Ediacaran frondose organism (*Aspidella*, cf. Gehling et al.,
240 2000; Supp. Fig. S2.5). This solitary disc is not directly associated with any of the traces, and
241 is 2–3 times larger than the width of the largest observed trail. Its interpretation is further
242 complicated by modern weathering and erosion resulting from its close proximity to the
243 ocean. Specimens of *Aspidella*, *Hiemalora* and *Charniodiscus* occur on bedding planes 1–2

m stratigraphically above and below the trace bed. The trace-bearing surface does not crop out elsewhere within the MPER, and it remains the only level within the Mistaken Point Formation in Newfoundland known to exhibit such traces, although recent discoveries from the younger Fermeuse Formation provide additional evidence for similar locomotory behavior within the Ediacaran of Avalonia (Menon et al., 2013; Liu and McIlroy, in press).

An important feature of the assemblage is its preservation of more than one type of impression. We recognise four main variants: (1) linear traces with crescentic transverse ridges in a central longitudinal groove; (2) plain, unornamented linear traces with a central longitudinal groove; (3) the possible cluster of traces seen in Figure 5; (4) simple discoidal pits, inferred to represent the resting trace of the trace maker. Further to previous comparisons of these Mistaken Point traces with late Ediacaran trace fossils (e.g., *Bergaueria*) and body fossils (e.g. *Palaeopascichnus*; see Liu et al., 2010a), we now consider additional macrofossils and ichnotaxa from the Ediacaran and lower Phanerozoic.

1. Paleontological Comparison

It has been suggested that the Mistaken Point trace fossils could be the impressions of the stems of poorly preserved fronds (Narbonne et al., 2012). This is considered unlikely, for several reasons. Where stems of frondose Ediacaran macro-organisms are seen to end in a terminal (holdfast) disc, this disc is usually larger than the associated stem, whereas our material possesses terminal pits of comparable width to the traces. Bending and curvature of the trace fossils is also inconsistent with the typically straight morphologies of frond stems. Finally, the stems of rangeomorphs and other related frondose organisms (e.g. *Charniodiscus* sp.) are rarely preserved in negative epirelief in the Avalon Terrane, seldom show marginal ridges, and do not have transverse structures along their length even when exceptionally

preserved (Brasier et al., 2013a). It would also be highly unusual not to find associated frondose architecture, given the style of preservation typically seen in the Avalon region (Narbonne, 2005). Flexure creases seen in *Rangea* specimens from Namibia (Vickers-Rich et al., 2013, fig. 7.5) would not be expected to form down the entire length of a preserved stem, and may be expected to be aligned in the current direction on a bedding plane subject to the influence of currents.

In recent years, a variety of tubular body fossils have been found in Ediacaran strata (e.g., Droser and Gehling, 2008; Sappenfield et al., 2011), possessing features such as basal circular discs and transverse segmentation at scales similar to those seen in our material. Of these cited studies, the presence of transverse crescentic ridges in some of our specimens is inconsistent with the diagnosis of *Somatohelix* (cf. Sappenfield et al., 2011), whereas a lack of rounded sub-rectangular units running along the length of the specimen rules out *Funisia* (cf. Droser and Gehling, 2008). Although some of our unornamented specimens do resemble *Somatohelix*, they do not show the sinuosity considered typical of that form. *Corumbella werneri*, a tubular body fossil described from Brazil, displays similar maximum dimensions to the Mistaken Point traces, but has numerous straight internal bars, spaced ~0.5 mm apart (Babcock et al., 2005). *Corumbella* also possesses an external central groove running along the length of its tube (Babcock et al., 2005), a feature not observed in any of the Mistaken Point specimens. Tubular body fossils such as *Gaojiashania cyclus* (Lin et al., 1986) from China are demonstrably composed of a series of articulated discs, which became disarticulated following the death of the organism (Cai et al., 2010; Cai et al., 2013). There is no evidence of such disarticulated segments of body fossils in the Mistaken Point assemblage. External tube ornamentation and regularly-spaced straight internal ridges, not seen in our material, are also features of *Calyptrina striata* (Sokolov, 1967); of a tubular form of similar dimensions preserved as a carbonaceous impression in the upper Doushantuo

Formation of China (Xiao et al., 2002, figs. 2.3–2.6); and of tubular fossils from the western United States (Hagadorn and Waggoner, 2000). Furthermore, clear differences exist between the Mistaken Point material and these previously described Ediacaran tubular body fossils. The presence of marginal sediment ridges, combined with clear truncations at cross-over points (Fig. 3D) rather than superimpositions, strongly suggest a trace fossil rather than tubular body fossil origin for the Mistaken Point material (cf. Jensen et al., 2005). Evidence for arcuate rather than straight transverse markings, widening diameters at points of curvature, and a lack of branching, is also inconsistent with typical preservation of many tubular body fossils (cf. Droser et al., 2005; Jensen et al., 2005, 2006; Liu et al., 2010a; Tacker et al., 2010).

2. Ichnological comparisons

The Mistaken Point traces with transverse ridges bear a passing resemblance to the 'lower surface expression' of the mainly Cambrian ichnotaxon *Plagiogmus*, but do not possess additional morphological traits at multiple levels within the sediment seen in that ichnogenus (McIlroy and Heys, 1997). Our material also lacks longitudinal furrows or ridges, ruling out comparison with impressions assigned to ichnogenera such as *Aulichnites*, *Bilinichnus*, and *Protovirgularia* (Häntzschel, 1975). The absence of tight meandering or coiling removes from consideration the mainly Ediacaran–Cambrian ichnotaxa *Cochlichnus, Nenoxites* and *Torrowangea* (the latter also requires regular constrictions), while the curvilinear, unbranched furrows of *Helminthoidichnites* Fitch 1850, although present in latest Ediacaran sedimentary successions (e.g., Hofmann and Mountjoy, 2010), are generally narrower, and show none of the internal structure present in our specimens with transverse ridges. *Helminthoidichnites* does however provide a compelling comparison for our unornamented variants.

Other horizontal surface trails possessing internal transverse ridges exhibit morphologies that are not compatible with those seen at Mistaken Point. The transverse ridges of *Psammichnites* often meander and do not meet the lateral margins of the trace (e.g., Seilacher, 2007), and those of *Neonereites* contain pellets, which we do not observe (e.g., Häntzschel, 1975, fig. 126.1). *Climactichnites*, common in Cambrian sections, can appear very similar (Getty and Hagadorn, 2009), but is generally much larger than our traces, and often possesses v-shaped transverse ridges and bilateral symmetry (Häntzschel, 1975).

Some Phanerozoic fossils with meniscate backfill also bear some resemblance to the present material. Cross-sections of actively backfilled cylindrical burrows such as *Taenidium* and *Muensteria* can be superficially similar (e.g. Bromley et al., 1999). There is, however, no evidence that the Mistaken Point specimens represent a cross section through a tubular feature, or extend into the sediment – they appear to be entirely surficial traces. Evidence to date suggests that meniscate backfill is a uniquely Phanerozoic trait (cf. Brasier et al., 1994; Brasier et al., 2013a; though see also Rogov et al., 2012).

Perhaps the closest morphological resemblance we have found for the transverse-ridged Mistaken Point trails is in the Paleozoic ichnogenus *Archaeonassa* Fenton and Fenton 1937, particularly a specimen figured by Buckman (1994, fig. 2A). However, despite possessing lateral ridges and the possibility of hemispheric transverse ridges in a central zone, *Archaeonassa* exhibits a wide range of plasticity in the morphology of the internal transverse ridges (Buckman, 1994). *Archaeonassa* has been recognised within Ediacaran successions previously, and has been interpreted by some to be an under-mat mining trace (Fedonkin et al., 2007, fig. 459). Although its typical Phanerozoic depositional environment is inconsistent with the observed sedimentological regime at Mistaken Point (intertidal, cf. Häntzschel, 1975), we consider that from a morphological viewpoint, *Archaeonassa* is the ichnotaxon that

exhibits the closest similarities to our material, and we therefore designate Mistaken Point specimens with transverse ridges ?*Archaeonassa*.

Meanwhile the cluster of trace-like impressions (Fig. 5), being a single example, can only be noted as an intriguing specimen that hints at the potential for as yet unrecognised complexity in the behaviour of organisms in deep marine environments at this time. The association could represent 1) locomotion or feeding from a central point, as seen in many modern gastropods, echinoderms on hardground surfaces (Gibert et al., 2007), and infaunal annelid taxa feeding from a semi-permanent burrow (e.g., nereid polychaetes in Herringshaw et al., 2010); 2) an association of several trace makers around a central point, possibly a foodstuff; or 3) coincidental occurrence of multiple linear trace fossils or similar impressions. We decline to speculate further about the behavior exhibited by this association at present, but it is interesting enough to warrant inclusion in this discussion, and further study.

In light of these observations, we therefore suggest that the Mistaken Point trace fossils could be variously assigned to the existing ichnogenera *Archaeonassa* (specimens with transverse ridges, e.g., Fig. 3B, D; Fenton and Fenton, 1937), and *Helminthoidichnites* (trails lacking transverse ridges, Fig. 3C; Fitch, 1850). However, due to the reasons outlined above regarding inconsistencies with published examples of each ichnotaxon, at present we feel it is sufficient to retain their description as 'simple horizontal surface traces'.

An important point to note is that trace fossil morphology can be influenced not only by organism and type of behaviour (e.g., Trewin, 1976), but by extrinsic factors such as environmental conditions and preservational processes (Knox and Miller, 1985). It has been demonstrated that sediment cohesiveness can play an important role in the depth of modern molluscan traces, and also in influencing the morphology of transverse ridges such

365 molluscs create (Knox and Miller, 1985). Those same authors also note that individual
366 modern traces can exhibit several different morphological characteristics along the length of
367 an individual specimen (Knox and Miller, 1985, fig. 1E). Such findings raise the possibility
368 that although we have treated them separately here, the Mistaken Point unornamented
369 specimens, and those with transverse ridges, could have been created by the same organism,
370 with their morphological differences resulting from minor sedimentological or behavioral
371 variations. Displacement of surficial sediment in the majority of the traces suggests that they
372 were formed at the sediment-water interface, rather than by under-mat miners (*sensu*
373 Seilacher, 1999). None of the many thousands of rangeomorph and related fossil impressions
374 preserved in Ediacaran biotic assemblages worldwide have ever been found directly
375 associated with trace fossils. As such, it is considered highly unlikely that a member of the
376 frondose Ediacaran biota was responsible for the formation of these impressions.

377

378 ## 3. Experimental comparisons with modern trace makers

379 From an evolutionary perspective, it is desirable to determine the type of organism that
380 created the Mistaken Point traces. It has previously been shown that the forms with transverse
381 ridges are morphologically similar to impressions produced in experimental settings by
382 modern actinian sea anemones (Liu et al., 2010a). Actinians move by means of hydrostatic
383 inflation of their basal pedal disc (Parker, 1916; Supp. Fig. S3.1), which is effected by
384 contraction and relaxation of muscular fibers (Batham and Pantin, 1951). Variations in the
385 width of certain traces (e.g. Fig. 3D) can be explained by movement of an organism with a
386 hydrostatic skeleton more readily than by organisms with a more 'constrained' musculature
387 (e.g. bilaterians). Whilst we remain of the opinion that actinian-like inflation is the most
388 parsimonious explanation for their mode of formation, recent studies have revealed

389 alternative possibilities for the mechanism by which the Mistaken Point trace-makers could
390 have moved.

391 Our observations of a metazoan that moves across the sediment surface by means of
392 'shuffling' (the sand dollar echinoderm, Order Clypeasteroida, moving on its tube feet)
393 indicate that such a style of locomotion produces an impression that is laterally bounded by
394 ridges of displaced sediment, but with a completely smooth interior. Studies of organisms
395 that move by mucociliary creeping (e.g. ceriantharian anemones and platyhelminths; Collins
396 et al., 2000), demonstrate that such organisms cannot produce the internal transverse ridges
397 seen in the ornamented Mistaken Point trails. Modern mature examples of both organisms are
398 also generally too wide (>10 mm) to produce the unornamented trace fossils seen at Mistaken
399 Point.

400 Annelids have been noted to exhibit the retrograde monoaxial muscular contraction
401 used by molluscs (Lissmann, 1945b; McIlroy and Heys, 1997), but the circular shape of the
402 terminal disc impressions seen in most ornamented Mistaken Point specimens suggests that,
403 unless the circular discs represent vertical burrow openings, annelids are not responsible for
404 these structures. Locomotion of giant protists has been posited as an explanation for the
405 Mistaken Point impressions (Knoll, 2011), but while modern gromiids are capable of forming
406 centimetre-scale trace fossils with lateral levee-like ridges (Buchanan and Hedley, 1960;
407 Matz et al., 2008), there remain doubts as to whether such organisms could have formed the
408 transverse morphological features of sediment displacement seen in some of the Mistaken
409 Point trails (Liu et al., 2010a). The fossil record of such protists, despite their thick organic
410 test (e.g., Rothe et al., 2009), is cryptic at best. They cannot, however, be ruled out as
411 potential trace-makers for the simple Mistaken Point trace fossils (those without transverse
412 ridges), without further experimental study.

413 Modern gastropods are capable of forming surface locomotory trace fossils that
414 exhibit crescentic internal meniscae, and have been suggested as possible trace-makers for
415 the Phanerozoic ichnotaxon *Climactichnites* (Getty and Hagadorn, 2009). Those authors
416 noted that gastropod surface trails in modern intertidal environments are seldom preserved,
417 owing to the destructive actions of erosion and bioturbation (Getty and Hagadorn, 2009). At
418 Mistaken Point, neither the destructive actions of wave or tidal currents, nor pervasive
419 bioturbation, are considered to have significantly influenced the deep-marine seafloor,
420 although turbidity and contour currents may well have frequently perturbed the seabed.

421 The resting body trace of the *Climactichnites* trace-maker is bilaterally symmetrical
422 and generally elongate (Getty and Hagadorn, 2009; though see Yochelson and Fedonkin,
423 1993); a morphology that contrasts with the broadly circular impressions seen at the
424 termination of some Mistaken Point trace fossils (after accounting for tectonic elongation; cf.
425 Fig. 4C). The waves of muscular contraction utilised by the modern gastropod *Viviparus* can
426 form transverse ridges like those of *Climactichnites* during locomotion under sub-aerial
427 conditions (Getty and Hagadorn, 2009). It is also noted that modern gastropods utilise a
428 variety of physical methods to move, including a range of 'stepping' motions (Lissmann,
429 1945a), and are not restricted to peristaltic muscle contractions.

430 In summary, these findings suggest that locomotion observed in modern protists and
431 annelids cannot explain the observed trails with transverse ridges at Mistaken Point (see
432 Table 2). Conversely, actinian/molluscan styles of locomotion could feasibly explain the
433 features observed in the Mistaken Point trace fossils, although this cannot be used to infer the
434 taxonomic affinities of the trace maker, nor extend the range of the Actinia and Mollusca. We
435 merely suggest that the biomechanics evidenced by the traces suggest a muscular eumetazoan
436 trace-maker. In contrast, we have observed modern worms, gastropods, and even caterpillars
437 forming smooth, unornamented traces of the size we describe from Mistaken Point. Those

bilaterian taxa are potential analogues for the creators of these impressions, but the morphological simplicity of the smooth un-ridged subset of the Mistaken Point traces cannot preclude formation by primitive organisms, such as protists.

The rarity of ichnofossils preserved within the Conception and St. John's Groups of Newfoundland could be explained by them being washed in from shallower depths (Liu et al., 2010a), by them requiring unusual taphonomic conditions, or by the tracemakers simply being rare components of these assemblages (Liu and McIlroy, in press). Shallow water traces of ~565 Ma are not currently known (the earliest examples being the ~560 Ma Fermeuse Fm., and the Upper Blueflower Fm. of NW Canada; Menon et al., 2013; Carbone and Narbonne, 2014; Liu and McIlroy, in press), but we note that very few shallow-marine successions of 580–560 Ma have been documented or studied.

The traces we describe are amongst the oldest evidence for locomotion by muscular metazoans, and it is becoming apparent that behavioural complexity gradually increased throughout the latest Neoproterozoic between 560 and 541 Ma (reviewed in Carbone and Narbonne, 2014; Liu and McIlroy, in press), likely driven by the evolution of bilaterian organisms (cf. Narbonne et al., 2014). Our current understanding suggests that the appearance of the earliest Ediacaran macro-organisms pre-dated that of metazoan trails by around 15 million years, with bilaterian burrowing appearing another 5–10 million years later. Continued research into these trace fossil assemblages, and their relationship to communities of Ediacaran taxa, may eventually permit constraint of the phylogenetic affinities of some of those enigmatic organisms.

CONCLUSIONS

A late Ediacaran bedding-plane at Mistaken Point, Newfoundland, in deep-marine sedimentary facies, records a variety of impressions that are considered ichnological on the basis of their morphology. Two different types of locomotion trace are evidenced, some in association with circular pits that we interpret as the resting trace of a trace-maker. Specimens with crescentic transverse ridges are morphologically similar to *Archaeonassa*, whereas specimens with plain interior furrows are comparable to *Helminthoidichnites*. Possible evidence for more complex behavioral activity is tentatively documented from a single clustered association of trace-like impressions.

Experimental, paleontological and ichnological comparisons indicate that the *Archaeonassa*-like Mistaken Point traces were likely to have been produced on or very close to the sediment surface, by an organism with basal locomotory musculature, most likely arranged within a circular disc. The basal musculature was capable of exerting force upon the surrounding sediment in a controlled and repetitive manner, often in a direction opposite to that of forward motion. This is evidenced by the crescentic transverse ridges of sediment, which mark the posterior impressions of the organisms.

Eumetazoans are the only extant creatures known to possess tissues with the ability to apply the forces required in an appropriate manner to form the traces with transverse ridges. The creators of these trace fossils are thus postulated to be of eumetazoan grade. Although we cannot state with certainty the specific phylum to which the trace-makers belonged, the Mistaken Point ichnofossil assemblage provides strong evidence for the presence of complex, muscular animals, potentially utilising more than one method of locomotion, in late Ediacaran marine assemblages of approximately 565 Ma.

ACKNOWLEDGEMENTS

The authors would like to thank the Oxford University Museum of Natural History for housing casts of this material, and Sören Jensen, Jim Gehling, Robert MacNaughton and one anonymous reviewer for providing comments that have improved the quality of this manuscript. We thank the Parks and Natural Areas Division, Department of Environment and Conservation, Government of Newfoundland and Labrador for granting permits to conduct research within the MPER. This research was supported by NERC doctoral studentships to AGL (2007–2011) and JJM (2011–present), and a Henslow Junior Research Fellowship from Girton College to AGL. DM also acknowledges financial support from NSERC. Readers are advised that access to the Mistaken Point Ecological Reserve Fossil Protection Zone for research is by scientific permit only – contact the Reserve Manager for further information.

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728

729

730 FIGURE AND TABLE CAPTIONS

731 **FIGURE 1**—A map and stratigraphic column indicating the location of the trace-bearing bed
732 (following Liu et al., 2010a, fig. 1). Stratigraphic column (not to scale), follows Williams &
733 King, 1979. A) Newfoundland, eastern Canada. B) The Avalon Peninsula of south-eastern
734 Newfoundland. C) The Mistaken Point Ecological Reserve (MPER). The Mistaken Point
735 trace fossil bed is represented by the black star on the southern side of Mistaken Point itself.
736 For the exact location of the site, please contact the Reserve Manager of the Mistaken Point
737 Ecological Reserve. Dates are taken from Benus (1988), and Van Kranendonk et al. (2008).

738

739 **FIGURE 2**—Sedimentology of the trace bearing bed, looking NNE. The trace fossils lie
740 directly above a turbidite, here labelled according to the terminology of Bouma (1962), and
741 beneath a thin, coarse-grained pyritic tuff (visible as a thin brown layer covering the bedding
742 surface). Scale bar length = 50 mm.

743

744 **FIGURE 3**—A selection of trace fossils from the upper Mistaken Point Formation, Mistaken
745 Point, Newfoundland. Dark brown/grey patches are regions of unweathered volcanic tuff. A)
746 Two trace fossils lacking internal transverse ridges. B) The longest trace on the bedding
747 plane, showing transverse hemispheric ridges running down its length, and ending in a
748 terminal negative-relief disc (arrowed). Specimens in A and B can be found on cast OUM ÁT
749 418/p. C) Two simple trace fossils exhibiting cross-cutting relationships, the horizontal one
750 ending in a terminal disc (arrowed). Photograph from cast OUM ÁT 421/p. D) A series of at

751 least four traces, clearly showing several directions of movement and cross-cutting
752 relationships (arrowed). Cast OUM ÁT 421/p. One shows a prominent pit at its end (at left).
753 All scale bars = 10 mm.

754

755 **FIGURE 4**—Orientation data for the impressions preserved on the Mistaken Point trace
756 fossil horizon. A) Orientations of trace fossils showing transverse ridges, plotted as
757 proceeding in the inferred direction of motion (towards concave face of the transverse
758 internal crescents). n = 29, maximum bin value = 4. B) Orientations of all non-ornamented
759 traces. Note that for these traces, direction of motion cannot be easily determined, and they
760 may run at 180° to the documented orientation. The values have therefore been plotted twice,
761 with 180° added to all of them, to produce a mirror image to reflect this uncertainty. n = 53,
762 maximum bin value = 7. C) Orientations of the long axes of the negative relief 'pits' found
763 on the bedding plane (indicating the primary axis of tectonic strain), n = 11, maximum bin
764 value = 3. Again, values here have been plotted as a mirror image to give a better indication
765 of the direction of strain.

766

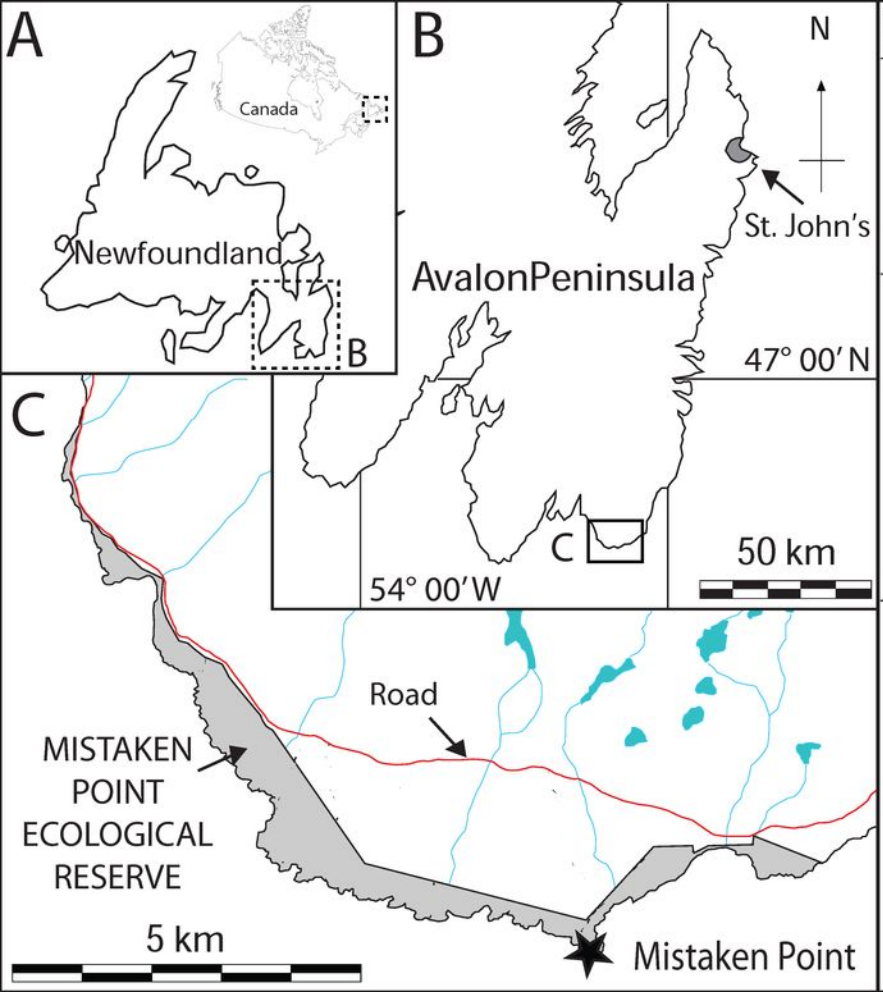
767 **FIGURE 5**—A cluster of trace-like impressions found at the eastern end of the outcrop,
768 seemingly emanating from a central point, which is composed of four small pits (arrowed).
769 Note impressions suggestive of repeated sequential motion over the surface to the left of the
770 pits. A cast of this specimen is housed at the Oxford University Museum of Natural History,
771 OUM ÁT.420/p. Scale bar length = 10 mm. Image shows the top surface of the bedding
772 plane.

773

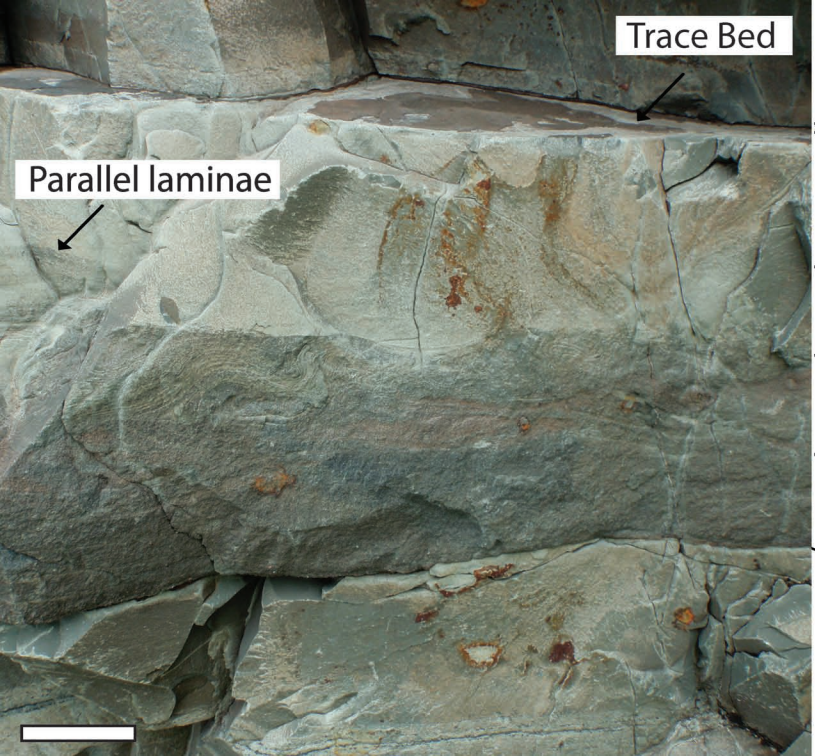
774 **TABLE 1**—A table comparing the characteristic features of the most likely abiological and
775 biological explanations for the formation of the Mistaken Point impressions. Y = yes, N = no.
776 The MPER impressions most closely match the features seen in *bona fide* Phanerozoic
777 surficial horizontal trace fossils.

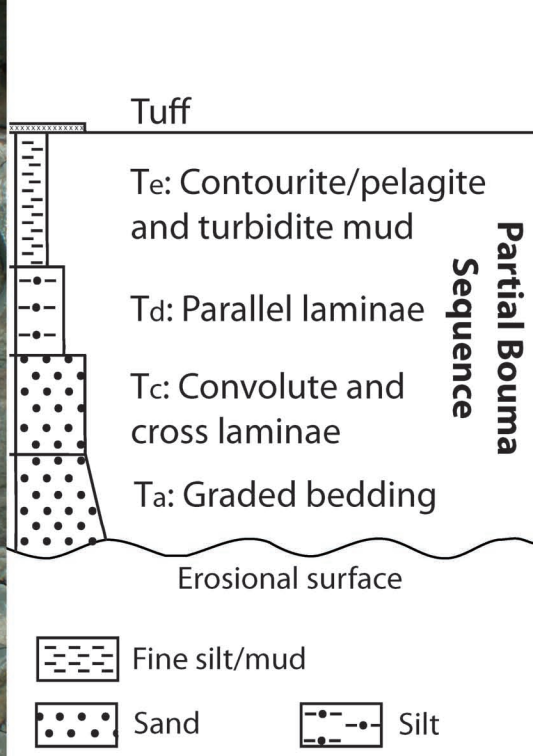
778

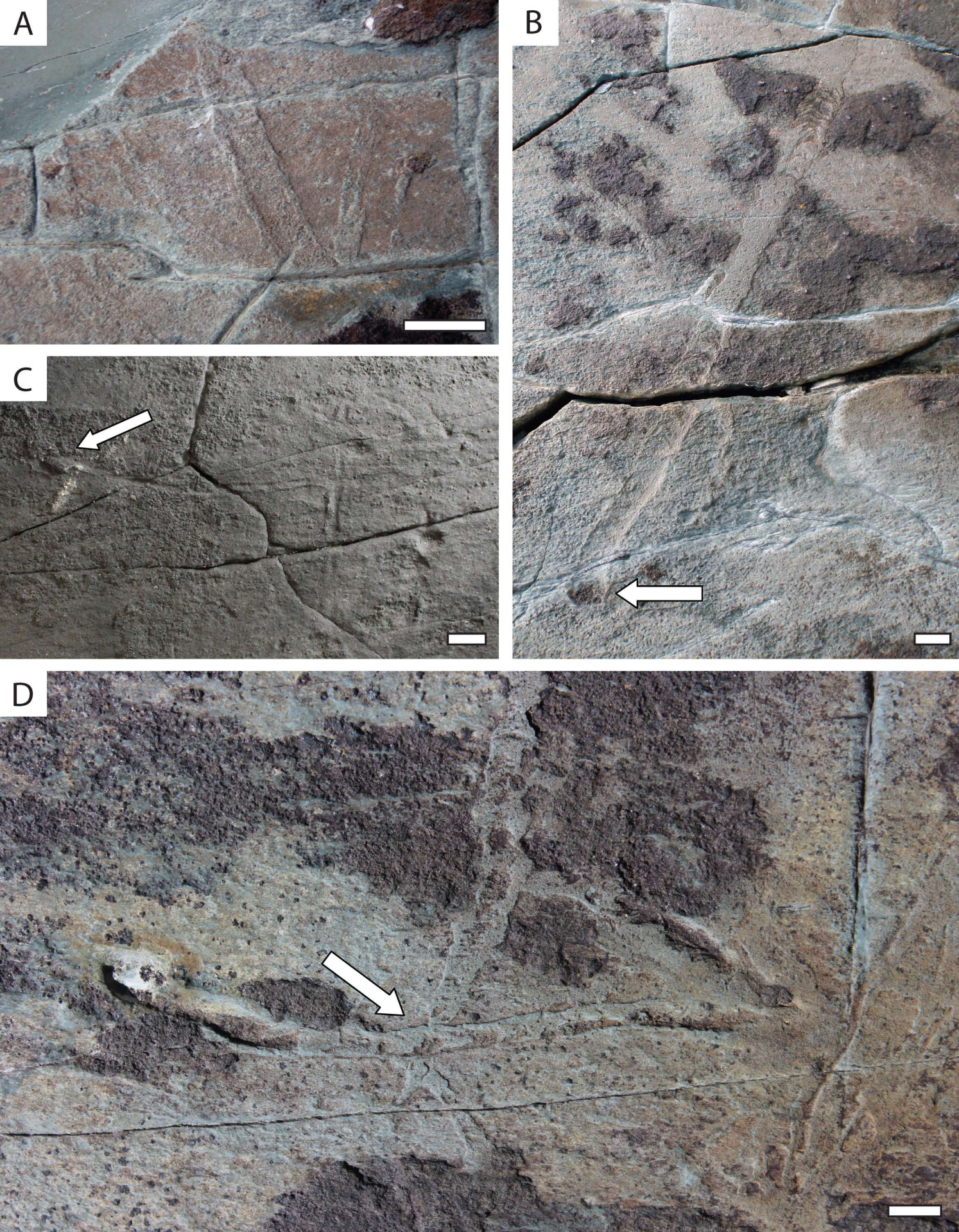
779 **TABLE 2**—A table comparing the diagnostic features that might be expected from protist,
780 actinian, annelid, and molluscan trace fossils with those seen in the Ediacaran Mistaken Point
781 fossils. Actinians and molluscs are the only groups capable of forming traces possessing the
782 combination of features seen in the trails exhibiting transverse ridges at Mistaken Point.

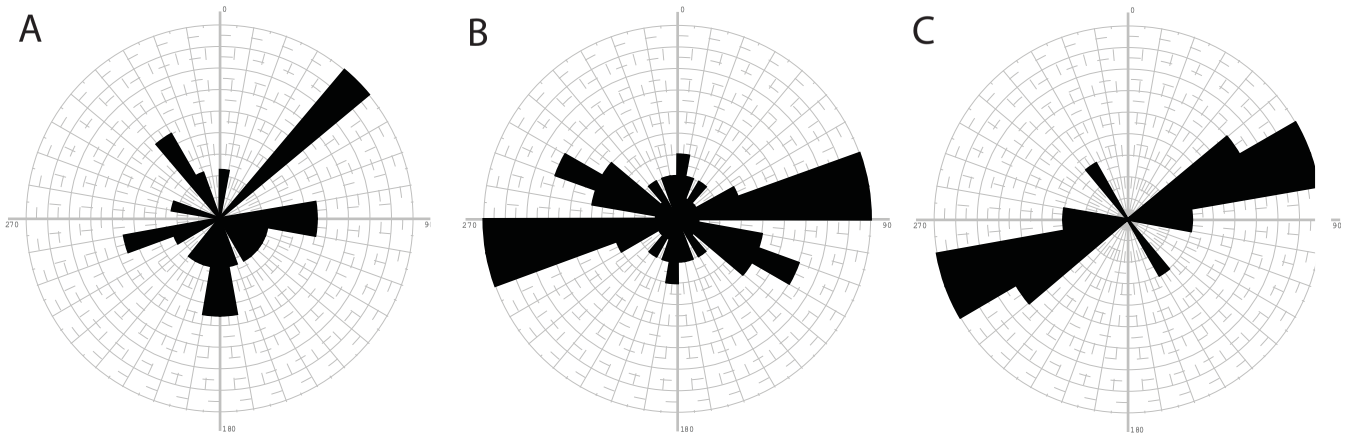


Group	Formation	Age
Signal Hill	Cape Ballard	
	Ferryland Head	
	Gibbett Hill	
	Cappahayden	
St. John's	Renews Head	
	Fermeuse	
	Trepassey	
Conception	Mistaken Point	565 ± 3 Ma
	Briscal	
	Drook	578.8 ± 0.5 Ma
	Gaskiers	
	Mall Bay	


Trace Bed
Parallel laminae


Tuff
Te: Contourite/pelagite and turbidite mud
Td: Parallel laminae
Tc: Convolute and cross laminae
Ta: Graded bedding
Partial Bouma Sequence
Erosional surface
Fine silt/mud
Sand
Silt


A
B
C
D


A
0
270
90
180
B
0
270
90
180
C
0
270
90
180

	Body fossils	Tilting traces	Tectonic fractures	Phanerozoic surface trace-fossils	Ornamented MPER impressions
Orientation	Variable	Consistent	Consistent	Variable	Variable
Curvature	Gentle	Gentle	None/sharp	Variable	Variable
Transverse ornamentation	Straight	Variable	No	Variable	Arcuate
Branching	Possible	No	Possible	Possible	No
Lateral ridges	No	Yes	No	Yes	Yes
Widens at points of curvature	No	Yes	No	Yes	Yes
Truncation or superimposition?	Sup.	Truncation	Truncation	Truncation	Truncation
Disarticulation	Possible	No	No	No	No
Vertical component	No	No	Yes	Yes/No	No
Mineralization	Possible	No	Yes	No	No
Clustering/ looping	No	No	No	Yes	Yes
Capable of possessing a terminal disc?	Yes	Yes	No	Yes	Yes

	Protists	Actinians	Annelids	Molluscs	Ornamented Mistaken Point Traces
Shape of expected terminal impression	Circular	Circular	Elongate (unless vertically burrowing)	Circular to elongate	Circular
Ability to produce internal transverse ridges?	No	Crescentic	No	Straight to crescentic	Crescentic
Lateral marginal ridges	Yes	Yes	Yes	Yes	Yes
Central ridge	Yes	No	No	No	No